

The Cretaceous marine squamate *Mesoleptos* and the origin of snakes

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SYNOPSIS. The poorly known marine squamate *Mesoleptos* is reassessed based on two previously known specimens and a newly referred specimen. The three specimens of *Mesoleptos zendrinii* share unique characters such as long, posteriorly tapering centra and distally straight but non-pachyostotic ribs. *Mesoleptos* had a narrow neck (and presumably small head), long laterally compressed body, and small fore- and hindlimbs. Phylogenetic analysis suggests that *Mesoleptos* is the nearest relative of snakes; this phylogenetic position is consistent with its morphology being intermediate between typical marine squamates (e.g. mosasauroids) and primitive marine snakes (pachyophiids). However, this interpretation remains tentative because *Mesoleptos* is very poorly known, and many of the characters uniting it with mosasauroids and primitive snakes are correlates of marine habits and/or limb reduction.

INTRODUCTION

Whereas sea snakes (Laticaudinae and Hydrophiinae) and marine iguanas (*Amblyrhynchus*) are the only truly marine squamates living today, there was a more diverse and very different radiation of such forms during the Cretaceous. These extinct marine squamates included the large monitor-like aigialosaurs and mosasaurs, the small, long-necked dolichosaurs, and the medium-sized limbed snakes *Pachyrhachis*, *Pachyophis*, and *Haasiophis*. These forms were suggested by workers in the late nineteenth and early twentieth centuries to be closely related to each other and to modern snakes (e.g. Cope, 1869; Boulenger, 1891; Gorjanovic-Kramberger, 1892; Nopcsa, 1908, 1923), a view which has been supported by some recent phylogenetic analyses (e.g. Scanlon, 1996; Caldwell 1999; Lee and Scanlon 2002; but see Tchernov *et al.* 2000; Rieppel and Zaher 2000).

One poorly known form that has been associated with this radiation is *Mesoleptos zendrinii* (Cornalia and Chiozza, 1852; Gorjanovic-Kramberger, 1892; Calligaris, 1988). *M. zendrinii* was a marine squamate with a rather elongated body, long ribs, and well-developed but rather small hindlimbs. It has been repeatedly associated with other contemporary marine squamates, largely on the basis of common habitat rather than any detailed analysis of morphology. Cornalia and Chiozza (1852) suggested affinities with '*Raphiosaurus*', based on a specimen (BMNH R32268) figured under this name by Owen (1842) but later referred to *Dolichosaurus* (Owen 1850a, 1851). Subsequent workers have commented on errors in the original description, though a full redescription of the type specimen has not appeared. Gorjanovic-Kramberger (1892) referred an additional specimen to *Mesoleptos* cf. *zendrinii*, discussed below, and referred this genus to the Varanidae, although acknowledging that it differed from other varanids in being highly aquatic. Nopcsa (1903) referred it tentatively to Aigialosauridae, and suggested that the moderate elongation of the trunk region relative to other known aigialosaurs was analogous to the independent elongation of the body in some mosasaurs such as *Chidastes*. Later, Nopcsa (1923) compared *M. zendrinii* with *Eidolosaurus trauthi*, including both in a subfamily Mesoleptinae within his broadly conceived Dolichosauridae (Mesoleptinae, Aigialosaurinae, Dolichosaurinae). He regarded the Mesoleptinae as intermediate

between two main lineages, one consisting of the Aigialosaurinae plus their probable descendants the Mosasauridae, and the other consisting of the Dolichosaurinae plus their probable nearest relatives – though not direct descendants – the snakes. Nopcsa's (1903, 1923) classifications still represent the most complete discussion of these forms to date, and are summarised by Calligaris (1988). However, no unambiguous derived characters have been proposed linking *Mesoleptos* with any of the other marine groups or with snakes, and these interpretations need to be critically examined.

Here, we identify a new specimen of *Mesoleptos*, compare it to previously known specimens, and use the combined material to infer the phylogenetic relationships and palaeoecology of *Mesoleptos*. *Mesoleptos* emerges as on the stem lineage leading to snakes, lying phylogenetically between marine lizards (mosasauroids, dolichosaurs, *Adriosaurus*) and primitive limbed snakes (*Pachyrhachis*, *Pachyophis*, *Haasiophis*). Garth Underwood's earliest research interests included the origin and evolution of snakes, and he has contributed to possibly the two most influential papers on this topic (Bellairs and Underwood 1951; Underwood 1967). The current paper is thus a small contribution to a field of inquiry that Garth Underwood helped establish.

Institutional abbreviations

HUJ PAL, Hebrew University of Jerusalem Palaeontological Collection; MCSNT, Museo Civico di Storia Naturale di Trieste; MNHN, Musée Nationale d'Histoire Naturelle, Paris; SAM, South Australian Museum.

DESCRIPTION OF NEW SPECIMEN

Material and horizon

The specimen consists of part and counterpart, but all morphological information is preserved on the part (Fig. 1A). Anterior vertebral column, ribs, shoulder girdle, and partial forelimbs. Locality: 'Ein Jabrud (Ain Yabrud), 7 km north-east of Ramallah (West Bank, Palestine) and 20 km north of Jerusalem. Stratigraphic horizon: Bet-Meir Formation (Lower Cenomanian; earliest Upper Cretaceous). Catalogued as HUJ-PAL EJ699.



Vertebrae

An articulated series of thirteen vertebrae (here referred to as vertebrae 1–13) is preserved, along with an isolated element on the lower left (vertebra 14). All vertebrae are exposed ventrally only; the surfaces of vertebrae 1–7 are weathered, while that of vertebra 11 is broken. The series 1–13 represents the anterior presacral part of the column. Vertebra 1, the anteriormost, is the smallest; size then increases gradually along the series such that the last is approximately twice the dimension of the first. The cervical-dorsal boundary cannot be precisely determined because the cartilaginous sternal contacts are not preserved. However, in typical lizards (anonymous referee, pers. comm.), the cervical-dorsal boundary lies slightly behind an abrupt increase in rib length. There is an abrupt change in the size and shape of the ribs between preserved vertebrae 5 and 6 (see below), suggesting the cervical-dorsal boundary was slightly behind this region, perhaps between vertebrae 7 and 8. Both shoulder girdles, however, are preserved around the level of vertebra 5, suggesting a slightly more anterior cervical-dorsal boundary.

The centra are all elongate, the length being approximately three times the width across the middle of each vertebra. They narrow sharply behind the transverse processes, and then more gradually posteriorly. All centra are procoelous; the anterior cotyle is deeply concave and the posterior condyle strongly convex. The articular surfaces of the condyles face posteriorly; part of the surface is sometimes exposed in ventral view, so they were at most only slightly inclined dorsally.

Subcentral foramina are visible on the ventral surface of most vertebrae: two are present on vertebrae 6 to 9, and one is present on vertebrae 10 and 12. They were presumably present on the other vertebrae but are not visible due to weathering and/or damage. Where two foramina are present on a single vertebrae, they are never bilaterally symmetrical and are often both on the same side of the midline.

A sagittal keel, extending along the posterior half of the centrum, is present on vertebrae 1 to 7. The keel terminates posteriorly in a prominent knob-shaped hypapophysis, which is, however, partly weathered away on all except vertebrae 6 and 7. The keels and (where preserved) the hypapophyses are more prominent on the anteriormost vertebrae and gradually decrease in size posteriorly. On vertebra 8, there is no keel. A weak hypapophysis may have been present, but this cannot be confirmed due to breakage. Both the keel and hypapophysis are absent from vertebrae 9 to 13, and the ventral surface is completely smooth.

A pair of transverse processes extend laterally from the anterior end of each centrum. These processes extend proportionally further laterally in the more posterior vertebrae: the diameter across the transverse processes is slightly less than the length of the centrum in the anteriormost vertebra, but slightly more in the posteriormost vertebra (Table 1). Most of the transverse processes on the anterior vertebrae are weathered ventrally, but at least one is complete on most of the posterior vertebrae. The articular surfaces of the processes are not fully exposed, but appear to have been single based on the morphology of the proximal ends of the ribs.

The isolated vertebra '14' does not fit onto either end of the

Fig. 1 (A) Photograph of the third known individual of *Mesoleptos* (HUPAL 699). (B) Specimen drawing. The anterior end of the specimen is to the top right. Unstippled areas represent areas represent broken bone. Scale bar = 2 cm. Abbreviations: **cor**, coracoid; **sca**, scapula; **cla**, clavicle; **hum**, humerus; **ep**, epiphyseal ossification; **v1** first (anteriormost) preserved vertebra; **p.vert**, isolated posterior vertebra; **r5**, rib of fifth preserved vertebra; **hyp**, hypapophysis.

Table 1. Measurements of HUI-PAL EJ699: midline length between rims of cotyle and condyle; width across transverse processes; straight-line length of rib. The vertebrae are numbered from the first preserved centrum.

Vertebra no.	Centrum length	Greatest width	Rib length
1	22	16	—
2	20.5	19	—
3	22	20	—
4	—	—	19.5
5	19	20	20
6	20	20.5	41
7	21	20	49
8	(16+)	23	49
9	22	23	59
10	23.5	24	73
11	(23+)	(24+)	89
12	25	31	(92+)
13	26	39	121
—	—	—	132
—	—	—	139
14	23	34.5	—

articulated series. It is too large to fit next to vertebra 1, and furthermore could not be a cervical as it lacks the mid-ventral keel and hypapophysis. However, it is too small to fit next to vertebra 13. As in most squamates, after reaching maximum size (at or past vertebra 13), the centra must have again gradually decreased in size towards the posterior end of the dorsal region. The isolated vertebra appears to belong to this region. Its surface is worn in a manner that suggests there were laterally paired ventral mounds or processes defining a median longitudinal trough on the posterior part of the centrum.

Ribs

Ribs are preserved in association with vertebrae 4 to 13. Only the left rib (right in ventral view) of vertebra 4 is preserved. Both ribs are preserved in association with vertebrae 5 to 8. Only the left ribs are associated with vertebrae 9 to 11. Both ribs are associated with vertebrae 12 and 13, but the right ribs are displaced so that they overlie the left ribs and point anteriorly. Three additional ribs belonging to the next three (missing) dorsal vertebrae are also preserved; these are presumably right ribs based on their similar orientation to the right ribs of the last two preserved vertebrae.

The anteriormost preserved rib is associated with the 4th vertebra. It is short (only as long as the centrum) and smoothly curved. The shaft is oval in cross-section and uniformly thick throughout its length. Slightly longer ribs, of similar shape, are associated with the 5th vertebra. The next pair of ribs, associated with the 6th vertebra, are much longer and quite different in shape. The distal end of the left rib (right in ventral view) is weathered away; the right rib is complete and its proximal half is smoothly curved, but the distal half is nearly straight. The more posterior ribs are similar in shape, except that the curved proximal portion occupies progressively less and less of the shaft. By vertebra 13, the curved portion only occupies the proximal one-fifth of the shaft.

The articular surfaces are visible on the left ribs associated with vertebrae 7, 8, 10 and 13, and on the second of the three isolated ribs. The ribs are all single-headed. The anterior ribs are flared at the proximal end and then nearly uniformly thick throughout their length, while more posterior ones have a distinct neck proximally before becoming thickened in the region of greatest curvature, then gradually tapering distally in the straight part of the shaft. The distal ends are truncated squarely where they joined the costal cartilages,

which are not preserved.

Approximate measurements of the vertebrae and ribs (Table 1) show a more or less steady increase in dimensions from vertebra 1 to 13, continued in the ribs belonging to the next two missing vertebrae (both ends of the last known rib are incomplete or obscured and its length is therefore not measurable). As noted above, the posteriormost preserved ribs cannot belong to vertebra 14, which is from the posterior trunk (abdominal) region.

Shoulder girdle and forelimb

Both scapulocoracoids are preserved in medial view. The right is complete except for the dorsal scapular blade, while the left is partly covered by a rib and is missing the distal (anterior) end of the procoracoid process. A curved strip of bone adjacent to the left scapulocoracoid is probably the left clavicle. The left humerus is preserved in proximal dorsal view. All appendicular elements are very small in proportion to the axial elements.

The scapula is a simple, rectangular plate; the scapular blade is short. Its anterior margin is weakly concave; a scapulocoracoid emargination was thus present. The coracoid is single and bears two processes, and two emarginations. The more dorsal process is much longer and extends anterodorsally, forming the ventral margin of the scapulocoracoid foramen and the dorsal margin of the coracoid emargination that represents the anterior coracoid foramen. The ventral process is shorter and expanded distally. It forms the ventral border of the anterior coracoid foramen and the dorsal border of the emargination representing the posterior coracoid foramen. The ventral margin of the coracoid is smoothly convex, and the posterior margin is drawn out into a posteroventral spur. The probable clavicle is a tiny curved rod, tapered at each end. There is no ventromedial expansion or foramen. The humerus is relatively large compared to the shoulder elements, though still small compared to the axial elements. The proximal end is expanded and flattened. The entire articular surface is occupied by a large, semilunar epiphysis which caps the humerus. The distal end of the humerus is weathered.

COMPARISONS WITH SIMILAR TAXA

The specimen is clearly a squamate, as it possesses all the synapomorphies of squamates (Estes *et al.*, 1988) for which it can be coded: single-headed ribs, cervical vertebrae with hypapophyses, procoelous vertebrae, presence of anterior coracoid emargination. Admittedly, these are relatively few because the specimen is very incomplete, but still sufficient to make a firm identification. Among squamates, it is clearly different from most groups in possessing distally straight ribs. The only taxa that possess such ribs are *Mesoleptos*, *Adriosaurus*, *Acteosaurus*, and various groups of aquatic snakes. The specimen here is compared to these forms, and to some other superficially similar taxa to which it might be related.

Mesoleptos zendrinii

HUI-PAL EJ699 is extremely similar to *Mesoleptos*, which is known from two specimens. The type of *Mesoleptos zendrinii*, from the Upper Cretaceous of Comen, Slovenia, is an articulated series of dorsal, sacral and anterior caudal vertebrae with ribs and a partial hindlimb. The specimen has been illustrated as a lithographic plate (Cornalia and Chiozza, 1852: pl. 3) and an interpretive line drawing (Calligaris, 1988: fig. 2). Cornalia (in Cornalia and Chiozza, 1852) considered the specimen to be exposed in dorsal view, while Gorjanovic-Kramberger (1892) maintained it was exposed ventrally,

Table 2. Measurements of *Mesoleptos zendrinii* holotype (based on Cornalia and Chiozza, 1852: pl. 3), for comparison with data in Table 1. The vertebrae are numbered from the first preserved rib.

Vertebra no.	Centrum length	Greatest width	Rib length
1	—	—	45
2	—	—	—
2	—	—	75
4	12	—	90
5	13	—	116
6	12	—	120
7	12	18	125
8	12	20	119+
9	20*	23	124+
10	15	24	120+
11	15	25	120+
12	15	22	114

* there may be inaccuracies with the outlines of some vertebrae in the original figure, or this anomalous high value could reflect longitudinal separation of two adjacent vertebrae during partial disarticulation of the skeleton before fossilisation.

but in any case most of the vertebrae are bisected by the broken surface of the slab and are thus seen as cross-sections at various levels. The intervertebral articulations are not clearly exposed, and Cornalia found no indication that the vertebrae were procoelous, though Gorjanovic-Kramberger (1892) and later authors assumed that they must have been similar to the specimen in the Novak collection (discussed below). The type specimen could not be located in recent times: Calligaris (1988) was unable to confirm it was still in the Museo Civico di Storia Naturale de Milano (Milan).

The most anterior parts preserved of the type are strongly curved ribs which probably contacted the sternum, and the first vertebral fragments are associated with the fourth visible rib. Some small elements and fragments visible between the anterior ribs may include parts of the shoulder girdle and/or forelimb. Apart from the first few, the ribs are weakly curved proximally and nearly straight for the distal two-thirds of their length. The ribs are widest at the proximal articulation and are otherwise slender, with no trace of thickening (pachyostosis) more distally. Ribs in the posterior half of the trunk are displaced to point anteriorly, corresponding to bloating and maceration of the carcass proceeding most rapidly in the area of the viscera, and the most posterior ribs are either lost or not exposed. The outlines of the first 12 preserved vertebrae are nearly triangular, indicating that they are split horizontally through the middle or lower part of the centrum. From about the 13th preserved vertebra the outlines of the trunk vertebrae are expanded posteriorly as well as anteriorly and the neural canal is exposed, indicating a more dorsal position of the break; after the 22nd there is not much visible of the vertebral centra themselves. Prominent transverse processes are visible on vertebrae 24–27, and transverse grooves on the 24th and 26th vertebrae resemble lymph channels seen on the ventral surface of the sacral and anterior caudal vertebrae in *Varanus*, suggesting that the skeleton is exposed ventrally, and that the 24th and 25th preserved vertebrae are the sacra. After the first two caudals (26–27), represented by broad transverse processes of one side, there are indeterminate fragments of two more vertebrae, then indications of four vertebrae in lateral view showing elongate, near-vertical chevrons and a tall but antero-posteriorly narrow, slightly back-sloping neural spine. Traces of longitudinal elements under the transverse processes of the 25th–26th probably represent the ilium, slightly displaced posteriorly, medially and (if the orientation is correct) dorsally from its natural position. The femur is level with the probable sacra; the tibia and fibula are articulated, but incomplete distally.

The two referred specimens consist of HUI-PAL EJ699 and another specimen in the Museo Civico di Storia Naturale, Trieste (MCSNT 9962; locality and other collection details undetermined). The latter consists of a shorter but similar section of the skeleton to that in the type, exposed dorsally (Calligaris, 1988). Comparisons of the vertebrae are difficult due to the different parts and orientations of the skeleton in the different specimens, but all three specimens might share the derived character of unusually long, and posteriorly tapering, trunk centra. The shape of the centrum in the type can be inferred from the cross-sectional views of the vertebrae, which in some parts of the trunk show a similar outline to the ventral views in HUI-PAL EJ699, being wide across the transverse processes and narrowing steeply behind them to be almost parallel-sided posteriorly. In MCSNT 9962, where only the upper part of the neural arch and postzygapophyses are visible, the vertebrae are about 3/4 as long (between successive neural arches) as wide (across postzygapophyses), which is similar to proportions in the more posterior part of HUI-PAL EJ699.

All three specimens share a distinctive feature of the ribs in that the distal portion, representing most of their length, is nearly straight. This is interpreted as a derived condition corresponding to lateral compression of the trunk region, as in the pachyophiids and some other groups of thoroughly aquatic snakes. All three specimens also exhibit, as far as can be seen, complete but small girdles and limbs. The development of the forelimb and shoulder girdle in the current specimen matches the development of the pelvis and hindlimb in the type and MCSNT specimens of *Mesoleptos*. The shoulder girdle and forelimb in HUI-PAL EJ699 are relatively small, but complete in that all major elements are present. All ossified shoulder girdle elements except the interclavicle are preserved, while (based on the size and ossification of the humerus) most of the distal forelimb bones were present. This is consistent with the small but well developed (though incompletely preserved) sacrum, pelvis and hindlimb in the two previously known specimens of *Mesoleptos*. The observation that the shoulder girdle and forelimb in HUI-PAL EJ699 are both reduced in size but complete, as is the pelvis and hindlimb in *Mesoleptos*, further suggests they are the same or closely related species.

Thus, HUI-PAL EJ699 can be associated with the two known specimens of *Mesoleptos* because (1) they exhibit no significant differences from each other, though they all differ from all other squamates, (2) they have derived similarities in the ribs (otherwise found only in very different forms) and, less certainly, in the vertebrae and limbs.

'*Mesoleptos*' cf. *zendrinii*

Gorjanovic-Kramberger (1892: pl. III, fig. 4) reported a specimen in I. Novak's collection showing several articulated vertebrae with ribs, and fragments of some other elements, which he referred to *Mesoleptos*, close to *M. zendrinii*. The collection consisted of material from Cretaceous deposits of Isola di Lesina (Italian name for Hvar Island), Croatia (Gorjanovic-Kramberger, 1892). This was held after his death by his widow Antonia Novak (Kornhuber, 1901: 19) but the present location of this material is unknown (Calligaris, 1988). Gorjanovic-Kramberger interpreted the specimen as exposed ventrally, but the shape of contacts between condyles and cotyles visible in his figure suggest that the vertebra may actually be exposed in dorsal view but sectioned horizontally at the base of the neural canal; this would invalidate comparisons based on the supposed ventral surface, though not the overall outline, of the centrum. The shape of the centrum in the most complete vertebra is very similar to vertebrae 9–13 of HUI-PAL EJ699. The elongate and

posteriorly narrow centra have been regarded as diagnostic of *Mesoleptos*, and are not found in any other limbed squamates, though a similarly shaped centrum is present in some primitive snakes (e.g. *Lapparentophis*, Hoffstetter, 1960; *Patagoniophis*, Scanlon, 1993; *Coniophis*, Gardner and Cifelli, 1999).

Girdle and limb elements are also present in the Novak specimen; Gorjanovic-Kramberger (1892: 99) describes 'indistinct impressions' of the humerus, radius, ulna and two metacarpals, altogether measuring 93.3 mm in length. This must be less than the total length of the forelimb, because the elements are incompletely represented (the ends of the long bones are obscured and the humerus can not be compared in detail with HUI-PAL EJ699), but it can be concluded that a forelimb was present and equivalent in length to between three and four thoracic vertebrae, just as in the HUI specimen. Plate-like structures are also shown just anterior to the supposed humerus in Gorjanovic-Kramberger's figure, suggesting the posterior margins of a scapula and coracoid like those of the HUI specimen, although no useful details can be compared.

On the other hand the ribs, although long, are curved throughout their length. While the centrum length of the one well-preserved vertebra is about 31.5 mm, the length of the most complete rib (belonging to the preceding vertebra) is over 90 mm (Gorjanovic-Kramberger, 1892). These proportions seem to indicate a position deep within the dorsal region. In HUI-PAL EJ699, curved ribs only occur up to the anterior dorsal region while more posterior ribs are straight. Thus the Novak specimen apparently lacks this apomorphy shared by the type of *Mesoleptos zendrinii* with the MCSNT and HUI specimens (neither Gorjanovic-Kramberger nor subsequent writers have commented on this difference). It should therefore not be referred to *Mesoleptos*, but might possibly represent a species closely related to either *Mesoleptos* or the *Mesoleptos*-snake clade (see below).

Adriosaurus, Acteosaurus

Adriosaurus suessi Seeley, 1881 (Lee and Caldwell, 2000) and *Acteosaurus tommasinii* von Meyer, 1860 (considered identical by Nopcsa, 1923) are small marine lizards with distally straight ribs and thus, laterally compressed bodies. *Adriosaurus* is known from two specimens, from Upper Cretaceous deposits of Comen, Slovenia and Lesina (=Hvar), Croatia, while *Acteosaurus* is known from a single specimen from Comen. However, they both differ from *Mesoleptos* in lacking the distinctly small cervicals (relative to dorsals), in possessing proportionally larger limbs, proportionally shorter and wider dorsal vertebrae, and in exhibiting heavy pachyostosis of both dorsal vertebrae and ribs. They are also much smaller than *Mesoleptos*.

Eidolosaurus trauthii

Nopcsa (1923) described *Eidolosaurus trauthii* from a near-complete skeletal impression found during the demolition of a house in the Istrian region, i.e. in the same general region as Comen, but possibly within the present borders of either Slovenia, Croatia, or Italy (more precise locality details were not provided). This specimen is currently housed in the Geologische Staatsanstalt, Vienna but has yet to be completely prepared. Fragments of the skull are present in articulation with the vertebral column, so that the total number of presacral vertebrae can be determined as 34. Short, slender ribs were present on at least three posterior cervicals, but on the basis of a sharp increase in length and thickness between adjacent ribs (as there is no trace of the sternum), Nopcsa counted 11 cervical and 23 dorsal vertebrae. Two sacral and 48 or more postsacral vertebrae were also present. Nopcsa interpreted the type of *Mesoleptos zendrinii*

as also having 23 dorsal vertebrae. The numbers of cervical and trunk vertebrae in *Mesoleptos* and *Eidolosaurus* are therefore comparable. The relative femur length is similar in both, corresponding to the length of three middle dorsal vertebrae. However, there are also considerable differences: in *Eidolosaurus* the centra of trunk vertebrae are as wide as long, with no indication of a posterior taper; there is a median groove between paired ridges on the ventral surface throughout the trunk (the groove further divided by a median ridge in posterior vertebrae); all trunk ribs are strongly and uniformly curved and greatly thickened; and both the vertebrae and ribs are pachyostotic.

Nopcsa (1923: 107, footnote) also mentions 'An undescribed fossil discovered by Professor Jäkel, which came to my attention while this work was in press, shows 18 posteriorly tapering vertebral centra, which bear long, slightly curved, proximally club-shaped ribs. The specimen is 28 cm long. The vertebral centra show a shallow but well developed median longitudinal groove. The anterior centra are almost triangular and wider than long. The general habitus is *Mesoleptos*-like, but the ribs are somewhat pachyostotic. Probably this form is related to *Eidolosaurus*.' This may have been the specimen collected by Prof. O. Jäkel at Lesina which Kornhuber (1901: 3) mentioned and referred to *Carsosaurus*. It would be particularly interesting to compare this specimen with HUI-PAL EJ699, which also resembles *Mesoleptos* but has somewhat thickened ribs, but no illustration was provided and again the present location of the specimen is unknown (Calligaris, 1988: 117).

Dolichosaurs: Dolichosaurus, Coniosaurus, Pontosaurus

Dolichosaurus longicollis Owen, 1850a from the English Chalk (Owen, 1842, 1851; Caldwell, 2000) and *Pontosaurus lesinensis* (Kornhuber, 1873) from Hvar, Croatia, are elongate, Cenomanian marine squamates known from two or more articulated partial skeletons, and are thus important for comparison with *Mesoleptos*. They both clearly differ from HUI-PAL EJ699 and the other *Mesoleptos* specimens in the shape of the ribs (distally curved rather than straight), the more gradual changes in rib length and vertebral dimensions along the trunk, and greater number of dorsal vertebrae, all of which correspond to a more slender and cylindrical body form. Individual mid-trunk vertebrae of *Dolichosaurus* differ from those of *Mesoleptos* in being less massive, and having proportionally larger condyles and cotyles. Otherwise, they are similar in possessing broad transverse processes, a posteriorly cylindrical centrum, well-developed zygosphenes, a long neural spine, and absence of pachyostosis. Vertebral morphology of *Pontosaurus* can not yet be adequately compared because the specimens remain incompletely prepared (Calligaris, 1988). *Coniosaurus crassidens* Owen, 1850a (*Coniasaurus* Caldwell and Cooper, 1999, invalid emendation or sustained lapse) and *Coniosaurus gracilodens* Caldwell, 1999, occur in the same deposits as *D. longicollis* but comparisons are more problematic. Only very incomplete postcranial remains of *Coniosaurus* are known; the vertebrae are very similar to those of *Dolichosaurus*, and the two species are diagnosed by features of the jaws and teeth unknown in *Dolichosaurus*. Thus, one of the species of *Coniosaurus* might be synonymous with *Dolichosaurus* (Caldwell, 2000).

Pachyvaranus crassispondylus

Pachyvaranus was described from the Maastrichtian of Morocco (Arambourg and Signeux, 1952: 288–91, pl. 41) based on a small number of isolated vertebrae (MNHN PMC 1–4) and two doubtfully associated osteoderms (PMC 5–6), and originally referred to

Aigialosauridae. However, it has narrower condyles and cotyles, relatively longer centra and more prominent transverse processes than known aigialosaurs. This suggests it should be compared with HUI-PAL EJ699, which it resembles in size. The *Pachyvaranus* specimens are from marine phosphate deposits, and differ from HUI-PAL EJ699 in the thick and compact ossification of the vertebrae (pachyostosis). The vertebrae also differ in that the centrum of *Pachyvaranus* is triangular, tapering rather than nearly parallel-sided posteriorly, but this could be a result of pachyostosis; in other pachyostotic reptiles the centra are further expanded posterolaterally, and nearly rectangular. Further, the reported 'zygosphenes' is only a small triangular projection comparable to that of *Varanus*, which does not bear facets for articulation with a zygantrum on the preceding vertebra. Arambourg and Signeux considered possible affinities with dolichosaurs (ruled out by the lack of true zygosphenal articulations in *Pachyvaranus*) as well as aigialosaurs (noting differences including the narrower condyles). The lack of zygosphenes in *Pachyvaranus* also rules out affinities with aigialosaurs, since recent studies (Carroll and DeBraga, 1992) have demonstrated the presence of well-developed zygosphenes in aigialosaurs. However, affinities with *Mesoleptos* were not considered. No material other than trunk vertebrae (and doubtfully associated osteoderms) has been described for *Pachyvaranus*, and conversely the vertebrae of *Mesoleptos* are not fully known 'in the round', so that it is not yet possible to make detailed comparisons.

Pachyophiidae

Three long-bodied, limb reduced Cretaceous marine squamates have been referred to Pachyophiidae: *Pachyophis woodwardi* Nopcsa, 1923 (Lee *et al.*, 1999), *Mesophis nopcsai* Bolkay, 1925, and *Pachyrhachis problematicus* Haas, 1979 (Haas, 1980; Lee and Caldwell, 1998; Zaher and Rieppel, 1999). Haas (1979) originally included *Pachyrhachis* in Simoliophiidae, as did McDowell (1987) who also added *Pachyophis*; but of the two family-group names proposed by Nopcsa (1923), Pachyophiidae has page priority. There is now agreement that pachyophiids are snakes but their exact position within snakes remains debated (Zaher and Rieppel, 1999; Tchernov *et al.* 2000; Lee and Scanlon, 2002). These three taxa are extremely similar, and possess small heads, heavily pachyostotic mid-body vertebrae and ribs, and distally straight ribs indicating lateral compression of the trunk. Radovanovic (1935: 411) postulated that *Mesophis* was a terrestrial snake in which the very slender distal parts of the ribs had been straightened by pressure during fossilization. However, this hypothesis is very unlikely because ribs of similar shape occur consistently in otherwise undistorted specimens of larger pachyophiids, namely *Pachyophis* and *Pachyrhachis*, as well as in other marine taxa (see below).

The specimen described here is clearly not a pachyophiid because in all known pachyophiids the forelimbs and shoulder girdle are completely absent, and the mid-trunk ribs are heavily swollen (pachyostotic). Also, the centra are long and taper posteriorly, unlike the pachyophiid condition of short centra that are of constant width throughout. The transverse processes also extend much further laterally than they do in pachyophiids.

Haasiophis

A new limbed Cretaceous marine snake, *Haasiophis*, has been described and interpreted to have affinities with *Pachyrhachis* (Tchernov *et al.*, 2000) and by implication with pachyophiids as a group. However, certain cranial elements were apparently misidentified, and a reassessment of the morphology suggests that these taxa are not closely related, but are successive outgroups to

crown-clade snakes (Lee and Scanlon 2002). The postcranial elements of *Haasiophis* have yet to be properly described, making comparisons with *Mesoleptos* difficult. However, *Haasiophis* differs from HUI-PAL EJ699 in possessing heavy pachyostosis of the vertebrae, many more trunk vertebrae, and in completely lacking a shoulder girdle and forelimb.

Palaeogene Marine Snakes

HUI-PAL EJ699 can be confidently excluded from the following groups of Tertiary snakes with distally straight ribs based on presence of forelimbs and very different vertebrae. *Archaeophis* (Archaeophiinae) has long, proximally curved but distally straight ribs (Janensch, 1906), and the ribs of *Palaeophis* share this morphology (Owen, 1850b). However, the neural arch is narrow and high, the centrum approximately cylindrical and the transverse processes relatively small (Rage, 1984). In the complete skeleton of *Archaeophis proavus* there are over 450 trunk vertebrae and no traces of limbs or girdles (Janensch, 1906), and there is no indication of their presence in other less completely known species. *Anomalophis* (Anomalophiidae) has similar ribs (Janensch, 1906; Auffenberg, 1959) and also small transverse processes. However, the centra are long and gradually tapering, and the neural arches are narrow and depressed, except for a backslipping neural spine. Vertebrae of other early aquatic snakes (Nigerophiidae and Russellophiidae; Rage, 1984, Averianov, 1997) have features resembling the palaeophiids, acrochordids and colubroids to a varying extent, but no ribs or articulated skeletons are known and their relationships remain obscure.

Thus, the specimen HUI-PAL EJ699 can be associated most closely with *Mesoleptos*. However, it differs from the type of *M. zendrinii* (as described by Cornalia and Chiozza, 1852; compare Tables 1 and 2) in the ribs of the anterior thoracic region being considerably shorter relative to vertebral length or width: the ribs are also thick in the curved middle portion of the shaft rather than uniformly slender. This region of the body is not preserved in the other referred (MCSNT) specimen. If confirmed, these differences would indicate a considerable variation in body shape (analogous to the differences among known specimens of aigialosaurids) which might justify erection of a new species. However, the location and condition of the type and some other important specimens are currently unknown, and the putative differences cannot be directly confirmed. There remains a possibility that the description and figure of the type are inaccurate, as they seem questionable in a number of details, and that the two specimens are identical. Thus, we have refrained from any formal taxonomic decisions pending a more comprehensive search for the type, and simply refer the current specimen to *Mesoleptos* sp. indet.

RECONSTRUCTION AND PALAEOECOLOGY

Based on all three specimens, *Mesoleptos* can be reconstructed as follows (Figs. 1 and 2). Depending on where one draws the cervical-dorsal boundary, there are five to seven cervical vertebrae preserved in HUI-PAL EJ699, and as these do not include the atlas or axis there must have been at least seven to nine cervicals, and possibly several more. Seven to nine cervicals are plesiomorphic for squamates and occur in most terrestrial varanoids, aigialosaurs and some mosasaurs, while dolichosaurs, *Eidolosaurus* and some mosasaurs have increased from this number (Nopcsa, 1908, 1923; Caldwell, 2000). There are 23 trunk vertebrae in the type and thus at least 30 to 32 presacrales altogether (cf. 34 in *Eidolosaurus*), but not many more than this

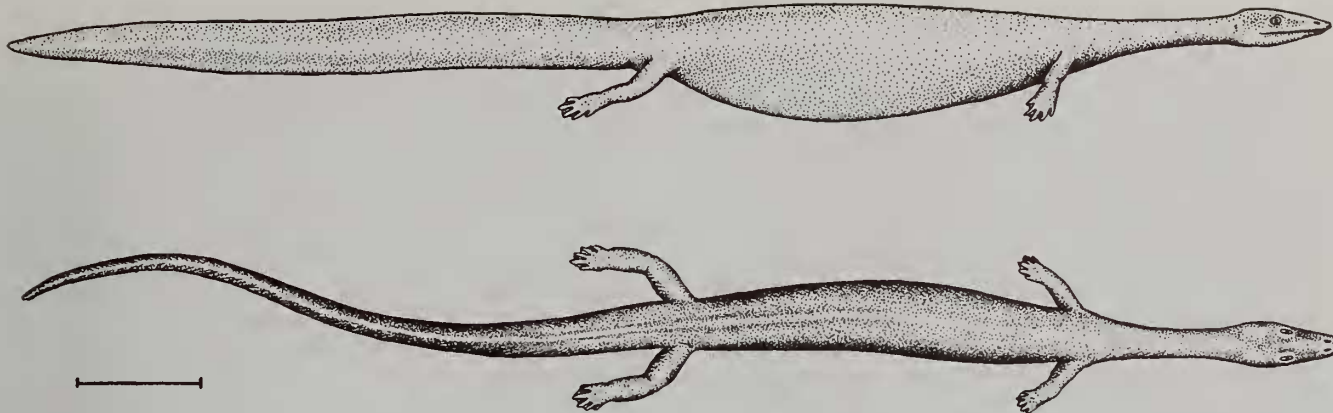


Fig. 2 Reconstruction of *Mesoleptos* in dorsal and lateral views. The head and tail are not known in any specimen and are thus conjectural. Note the long neck, long laterally compressed body, and short webbed limbs. Scale bar = 10cm.

unless the neck was unusually long. Short, curved ribs are present on most of the cervical vertebrae, implying a narrow cylindrical neck, which is similar to conditions in *Eidolosaurus* and some dolichosaurs, rather than aigialosaurs which have longer ribs on most of the cervicals. The cervical-thoracic boundary presumably lies around, or immediately posterior to, the sharp increase in rib length.

The anterior thoracic ribs are straight distally, implying a lateral flattening of the trunk region. Allowing for apparent variation between the three known specimens in the proportional length of the ribs, the ribs remain long throughout the mid-trunk region, where the largest vertebrae occur. Vertebral and rib dimensions increase steadily up to at least the tenth thoracic vertebra, are highest in mid-trunk and decrease, apparently more slowly, in the last ten or so presacra. These size gradients are stronger than seen in measured skeletons of *Varanus* and *Heloderma* (Scanlon, unpublished data), and far more conspicuous than in any other marine varanoids described. Unlike some aigialosaurs and all mosasaurs, there is not a long series of shortened posterior dorsal ribs. Rather, long, distally straight ribs continue at least to within the last five presacral vertebrae (as indicated by the MCSNT specimen; the most posterior ribs have been damaged or lost in both this and the type).

The cervical vertebrae bear prominent ventral keels and hypophyses, which are reduced on the first two thoracics and then disappear. The centra of the following thoracic vertebrae are smooth ventrally, but posterior trunk vertebrae apparently have laterally paired keels defining a median trough, a feature that also occurs in dolichosaurs, *Eidolosaurus* and some aigialosaurs (but often commencing more anteriorly in the trunk). The sacral vertebrae (in the MCSNT specimen at least) are shorter than the immediately preceding trunk vertebrae, and are fused (or at least very tightly articulated) together. Parts of the first few caudal vertebrae are present in the type, indicating a laterally compressed tail with elongate but antero-posteriorly narrow neural spines and chevrons.

The trends in vertebral size (length and width) and rib length indicate an animal with a relatively small head and narrow neck in relation to its body, similar to dolichosaurs and *Eidolosaurus*. The curved cervical ribs indicate that the cervical region of the animal was approximately round in cross-section. However, the distally straight dorsal ribs indicate that the trunk region of the animal was laterally compressed and very deep. These long ribs projected only a short distance laterally from the vertebrae before curving to extend downward (and obliquely backward) for most of their length. The girdles and limbs were rather small, although most elements were probably present; compared to adjacent vertebrae, both the femur

and humerus are relatively shorter than in aigialosaurs, but the forelimb was not as reduced as in dolichosaurs or *Eidolosaurus* (Fig. 2).

In comparison with the similar-sized aigialosaurs, *Pontosaurus* and species of *Varanus*, trends in vertebral size within the column of *Mesoleptos* are somewhat different. There is a local minimum of centrum length in the posterior cervical region, but the elongation of the anterior cervicals is much less pronounced than the condition in most *Varanus* spp. (a derived condition within that genus). Gradients of vertebral length and width within the thoracic and dorsal region are stronger than in any of the other taxa. The centrum is narrower posteriorly than in aigialosaurs, *Pontosaurus* and *Varanus*, indicating a condyle-cotyle joint of smaller diameter and surface area. This in turn suggests weaker compressive forces within the column, along with a less energetic style of locomotion and/or a greater capacity for lateral flexion of the neck and trunk. On the other hand, the combination of long transverse processes and long narrow centra increases both leverage and space for muscles connecting successive transverse processes, such as the *m. interarticularis* (cf. Mosauer, 1935; Gasc, 1974). These could then be of increased importance in lateral undulation, perhaps taking over in this role from longer muscles inserting on the ribs whose effectiveness would be decreased by lateral compression of the trunk. If the above interpretation of the affinities of the Novak specimen is correct, the derived vertebral morphology evolved before the lateral compression, so that this 'takeover' could happen via an intermediate where both sets of muscles were effective. Zygosphenes, considered to be of biomechanical importance in limiting twisting between adjacent vertebrae (Gasc, 1974), are well-developed (exposed dorsally in the MCSNT specimen) and articulate with zygantra in the preceding neural arches as in other aquatic varanoids and all snakes.

Among living squamates, the only forms with distally straight ribs (and thus laterally compressed bodies) are highly aquatic caenophidian snakes, such as file snakes (acrochordids) and sea snakes (laticaudine and hydrophiine elapids). This feature has rarely been discussed in extant snakes; Hoffstetter and Gayraud (1965) do not comment on any unusual features of the ribs in *Acrochordus* or *Enhydrina* (Hydrophiinae), though it was described in '*Enhydria*' (= *Lapemis*) *hardwickii* (Hydrophiinae) by Janensch (1906: 22). In *Acrochordus arafurae* (SAM R26956, R26966) the anterior ribs are robust and strongly curved, while those of the posterior half of the body are much more slender and only weakly curved except near the base. The pachyophiids – primitive marine snakes – also had a

similar morphology, which is functionally correlated with anguilliform swimming (Scanlon *et al.*, 1999; Lee *et al.*, 1999). It can thus be concluded that *Mesoleptos* was marine. This is also supported by the morphology of the posterior ribs. While they do not exhibit the histological features of true pachyostosis, they are nevertheless robust (in the MCSNT and HJ specimens) and might have served to reduce buoyancy, much like the pachyostotic ribs in other marine reptiles. The type of *M. zendrinii*, from the Comen locality, also comes from deposits dominated by marine fish (Gorjanovic-Kramberger, 1892) and is associated with aigialosaurs, dolichosaurs and pachyophiids. This also presumably applies to the MCSNT specimen (although its collection details have not been recorded it is probably from either Comen or Lesina). Marine habits of the present specimen are also implied by the position of the 'Ein Jabrud locality far from the palaeoshoreline (Scanlon *et al.*, 1999), and the articulated nature of the preserved elements suggesting *in situ* preservation.

The laterally compressed body and small limbs suggest that *Mesoleptos* swam primarily by lateral undulation, holding its limbs against its flanks (Carroll 1985; Lee 1999). In such forms, most of the propulsion occurs by movements of the tail, and to some extent the posterior region of the trunk. This is consistent with the observation that the posterior trunk region is most laterally compressed in *Mesoleptos* (the tail is unknown). The forelimbs and hindlimbs, however, were still large and well ossified enough to have been functional. They may have been used for slow locomotion ('walking') along the seabed, where (with the help of buoyancy) they could have supported the body. Alternatively, or additionally, they may have been used for forays on the shore.

PHYLOGENETIC RELATIONSHIPS OF *MESOLEPTOS*

All previous interpretations of the morphology and relationships of *Mesoleptos* were based either on poorly preserved and inadequately described material (the type), or on a composite of the type with the referred Novak specimen (Gorjanovic-Kramberger, 1892) which is clearly distinct from *M. zendrinii* in rib morphology. Gorjanovic-Kramberger's inclusion of *Mesoleptos* in Varanidae was 'phenetically' based on its long ribs, as distinct from the shorter and more uniform ribs of *Aigialosaurus* (as then interpreted) and dolichosaurs. However, he recognised it as marine in habits and thus by no means a typical varanid. Nopcsa classified *Mesoleptos* doubtfully as an aigialosaur (1903), but later placed it in a separate subfamily (Mesoleptinae) with *Eidolosaurus*, close to both aigialosaurines and dolichosaurines within Dolichosauridae (1923).

McDowell and Bogert (1954) returned *Mesoleptos* and *Eidolosaurus*, again doubtfully, to Aigialosauridae, but also briefly considered that they might be related to the living earless monitor, *Lanthanotus*. Hoffstetter (1955) also retained *Mesoleptos* as a possible aigialosaurid, while recognising *Eidolosaurus* as a dolichosaur and suggesting that *Pachyvaranus* might represent a distinct family. Romer (1956) placed both *Mesoleptos* and *Eidolosaurus*, with question marks, in Dolichosauridae.

The current state of understanding of these groups is perhaps best indicated by the fact that the systematic conclusion to Calligaris' (1988) review was formed by a summary of Nopcsa's (1923) classification, without substantial additions or revisions. That these groups have been poorly studied recently is highlighted by Carroll and DeBraga's (1992) statement that only five species had been assigned to Aigialosauridae, and did not mention either *Mesoleptos* (assigned to Aigialosauridae by Nopcsa, 1903, Camp, 1923, and

McDowell and Bogert, 1954), *Eidolosaurus* (assigned by Nopcsa, 1923, and McDowell and Bogert, 1954) or *Pachyvaranus* (assigned by Arambourg and Signeux, 1952).

The relationships of *Mesoleptos*, therefore, remain unresolved. While a robust assessment will have to await more complete material, a preliminary analysis is undertaken here. Morphological information from the MCSNT and HJ specimens (based on examination of specimens) and the type (based on published descriptions) was used in order to evaluate its phylogenetic relationships. *Mesoleptos* was added to the data matrix used in the most recent comprehensive analysis of squamates (Lee 2002); this matrix includes 248 osteological characters, used here, and addresses recent criticisms of various characters (Rieppel and Zaher 2000). Recently described (or redescribed) elongate marine squamates were also included in this matrix: *Pachyrhachis* (Lee and Caldwell, 1998), *Pachyophis* (Lee *et al.*, 1999), *Adriosaurus* (Lee and Caldwell, 2000) and dolichosaurs (*Coniosaurus* and *Dolichosaurus*; Caldwell and Cooper, 1999; Caldwell, 1999, 2000). *Coniosaurus* and *Dolichosaurus* are here combined into a single taxon, Dolichosauridae *sensu stricto*, based on the observations that the comparable parts of the two taxa appear almost identical, they overlap stratigraphically, and as noted by Caldwell (2000) one of the *Coniosaurus* species might be synonymous with *D. longicollis*. Character codings for all taxa (except *Haasiophis*) in this matrix, including the marine fossil forms, are based on direct examination of the material. As descriptions of the remaining marine squamates discussed above are dated, and they have yet to be restudied, they have not been included in the analysis. The full matrix is presented elsewhere (Lee 2002) and only the (new) character codings for *Mesoleptos* are listed here (Appendix 1). The full matrix (including *Mesoleptos*) used in this analysis has been deposited in TreeBase (<http://www.treebase.org/treebase/>).

The enlarged data matrix with *Mesoleptos* was analysed using the heuristic algorithm of PAUP* (Swofford, 1999) employing 100 random addition sequences. Two analyses were performed, with multistate characters ordered according to morphoclines where possible, or with all multistate characters unordered, to see if the phylogenetic analyses were contingent on assumptions of character state transitions. The degree of support for each grouping was ascertained by the support index (Bremer, 1988), calculated in PAUP using batch commands generated by TreeRot Version 2b (Sorenson, 2000). These commands were modified so that each heuristic search employed 100 rather than 20 random addition sequences. Nonparametric bootstrapping (1000 heuristic replicates each employing 100 random addition sequences) was also used to assess the robustness of each clade. As there were no fully specified a priori hypotheses for *Mesoleptos* and all other squamates, Templeton tests are inappropriate and were not performed (Goldman *et al.*, 2000).

Phylogenetic affinities

In the ordered analysis, three most parsimonious trees were found, each of length 672, consistency index = 0.46, retention index = 0.71. The strict consensus is shown in Fig. 3A, along with nodal supports. In the unordered analysis, 4 most parsimonious trees were found when only branches with unequivocal character support were retained, each of length 639, consistency index = 0.48, retention index = 0.71. The strict consensus is shown in Fig. 3B, along with nodal supports.

The basic topologies of the ordered and unordered consensus trees are similar to each other and largely unchanged from that the previous study (Lee, 2002), so that diagnoses of all the clades within Squamata are not repeated here. The characters diagnosing additional

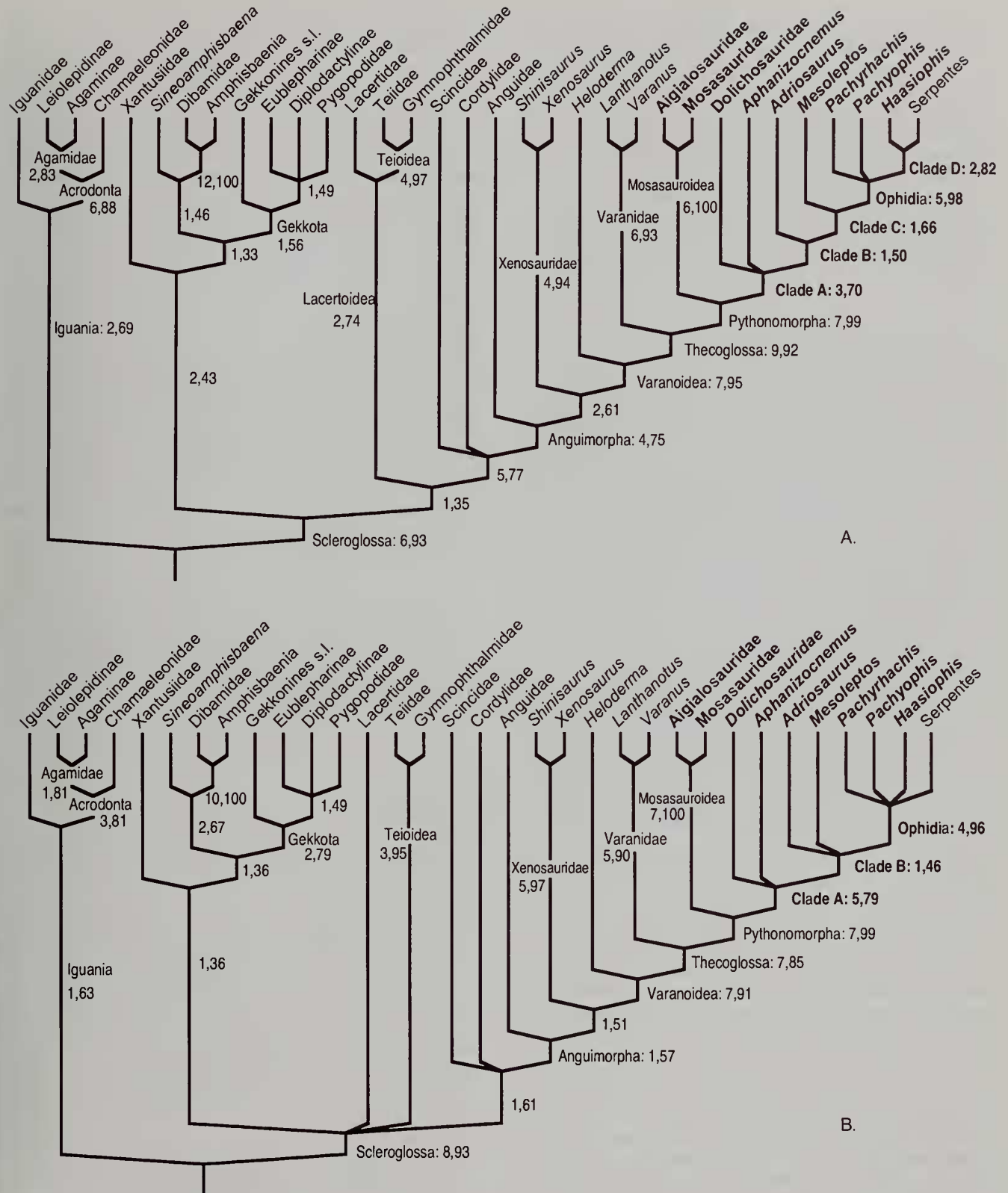


Fig. 3. The phylogenetic affinities of *Mesoleptos*, based on cladistic analyses of 248 characters across squamates. (A) Analysis with multistate characters ordered, strict consensus of 3 trees, length 672, consistency index 0.46, retention index 0.71. (B) Analysis with multistate characters unordered, strict consensus of 3 trees, length 639, consistency index 0.48, retention index 0.71. First number next to each clade refers to branch support (Bremer, 1988); second number refers to bootstrapping frequency. Clades immediately relevant to the affinities of *Mesoleptos* are in bold and are discussed in the text. The other more inclusive clades are discussed in Lee (1998). Aquatic terminal taxa are indicated in bold.

clades of immediate relevance to *Mesoleptos* are listed below. The character changes diagnosing these clades in the 'ordered' analysis under delayed transformation optimisation are listed in Appendix 2; the changes in the 'unordered' analysis are very similar, except that some clades collapse (compare Figs 3A and B). Unequivocal changes, i.e. those which occur under both delayed and accelerated optimisation, are indicated with an asterisk (*). Note that most characters diagnosing snakes (Ophidia) are equivocal because *Mesoleptos*, the sister group of snakes, is poorly known and nearly all the characters could apply to a more inclusive clade that also contains *Mesoleptos* (clade C). As discussed below, the clades are not strongly corroborated due to missing data and possible correlation of the supporting characters, and are thus not yet named formally.

EVOLUTIONARY IMPLICATIONS

The phylogenetic results imply that snakes arose from within a plexus of marine varanoids, an idea suggested initially by Nopcsa (1908, 1923) and later by Haas (1980). The aquatic hypothesis is often ascribed to Cope (1869), but Cope never suggested that the aquatic mosasaurs were ancestral to snakes: rather, he suggested that both had a close common ancestor, which might even have been terrestrial. However, critics subsequently misquoted Cope as suggesting that snakes evolved directly from mosasaurs and thus had marine ancestors, and then proceeded to argue that as snakes could not have evolved from mosasaurs (which possess numerous specialisations), they could not have had marine ancestors (e.g. Owen, 1877; Dollo, 1903, 1904; Janensch, 1906; McDowell and Bogert, 1954; Zaher and Rieppel, 1999). Nopcsa (1908, 1923) recognised and addressed the erroneous arguments of Owen and Janensch, and put forward a rigorous case for a marine stage in snake ancestry. More recently, by interpreting aigialosaurs as probable ancestors of snakes, McDowell and Bogert (1954) implicitly proposed a marine ancestry. In describing the second specimen of *Pachyrhachis* (=Ophiomorphus), Haas (1980: 191) stated that the fossil 'points to the fact that the snakelike body and loss of limbs did develop in a marine surrounding'. Despite this, the aquatic theory has in recent times been largely rejected in favour of the 'fossorial theory', i.e. that snakes evolved from small elongate burrowing lizards (e.g. Janensch, 1906; Walls, 1940; Bellairs and Underwood, 1951; Underwood, 1967; Rieppel, 1988; Greene, 1997). Thus, few modern studies rigorously surveyed marine varanoids and marine ophiomorphs for possible relationships with modern snakes.

This analysis indicates that the closest four to eight outgroups to modern (terrestrial) snakes are marine; the exact number varies depending on how the polytomies are resolved. The most parsimonious interpretation is that marine or at least semi-aquatic habits were primitive for pythonomorphs, and that snakes evolved in a marine or semi-aquatic environment and are secondarily terrestrial (Nopcsa, 1908, 1923; McDowell and Bogert, 1954; Haas, 1980). In order to maintain that the snake stem lineage was always terrestrial, between four and eight convergent invasions of marine habitats must be assumed to have occurred in mosasauroids, dolichosaur-like taxa, and basal snakes. The analysis further suggests that, of all the marine varanoids, *Mesoleptos* occupies a crucial phylogenetic position, as the nearest relative of snakes (Ophidia). If this is true, the similarities between *Mesoleptos* and primitive snakes are not convergent; these include such traits as a proportionally small head, long body, limb reduction, and lateral body compression. In these features, *Mesoleptos* appears inter-

mediate between the typical lizard-like marine varanoids (e.g. mosasaurs) and primitive marine snakes.

Two substantial caveats must be added to this interpretation. Apart from mosasaurs and aigialosaurs, all the marine varanoids are very imperfectly known. For instance, *Mesoleptos* can be scored for only 13% of characters, dolichosaurs for 35% and *Adriosaurus* for 38%. Such large amounts of missing information suggest that their positions cannot be very robust, a view confirmed by low bootstrap and Bremer supports. This missing information also reduces support throughout the tree, as the poorly known taxa can fit into many different places with only slight loss in parsimony. Additionally, many of the characters that unite dolichosaurs, *Adriosaurus* and *Mesoleptos* with mosasauroids and snakes, to the exclusion of other varanoids, are correlates of marine adaptation. Within this group (Pythonomorpha), many of the characters uniting dolichosaurs, *Aphanizocnemus*, *Adriosaurus* and *Mesoleptos* with snakes to the exclusion of mosasauroids are correlates of body elongation and limb reduction. Thus, the position of these poorly known taxa close to snakes might reflect a false signal caused by marine adaptation and body elongation, both features found in basal snakes. More complete fossil finds, and thus, information on characters not obviously correlated with habitat and body form, are required before their phylogenetic relationships can be conclusively ascertained and the early evolution of snakes clearly understood. The fundamental questions investigated by Bellairs and Underwood (1951) and Underwood (1967) regarding the affinities and ecological origins of snakes still await convincing answers.

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Appendix 1

Additions to the osteological data matrix of Lee (2002) used in this cladistic analysis. *Mesoleptos* was added to the taxon list and could be coded for the following characters.

Axial Skeleton

171. **Centra**. Not constricted anterior to condyle, i.e. condyle not wider than posterior end of centrum (0); slightly constricted anterior to condyle, i.e. condyle slightly wider than posterior end of centrum (1); greatly constricted anterior to condyle, i.e. condyle much wider than posterior end centrum (2). *Mesoleptos* 0.
172. **Vertebral articular surfaces**. Vertical, condyles (if present) facing posteriorly, much of the articular surface is visible in ventral view (0); slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articular surface is visible

- in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articular surface is visible in ventral view (2). *Mesoleptos* 0.
174. **Centra**. Notochordal, i.e. perforated by persistent notochord in adults (0); not notochordal, i.e. not perforated by persistent notochord in adults (1). *Mesoleptos* 1.
175. **Centra**. Amphicoelous (0); procoelous (1). *Mesoleptos* 1.
176. **Neural spines**. Tall processes (0); low ridges (1). *Mesoleptos* 0.
177. **Zygosphenes and zygantra**. Present (0); absent (1). *Mesoleptos* 0 (Visible on the MCSNT specimen).
179. **Intercentra on dorsal (thoracolumbar) vertebrae**. Present (0); absent (1). *Mesoleptos* 1.
180. **Number of presacral vertebrae**. 23 to 25 (0); 22 or fewer (1); 26 (2); 27 to 50 (3); 50 to 119 (4); 120 to 150 (5), 150 or more (6). *Mesoleptos* 3.
182. **Transverse processes of cervicals**. On anterior end of centrum (0); on middle of centrum (1). *Mesoleptos* 0.
183. **Hypapophyses on anterior presacrals**. Only extending to the posterior end of the sixth presacral at most (0); extending to the seventh presacral or beyond (1). *Mesoleptos* 1.
185. **Anterior presacral vertebrae** (excluding atlas and axis intercentra). Not sutured or fused to preceding centrum (0); sutured to preceding centrum (1); fused to preceding centrum (2). *Mesoleptos* 2.
186. **Anterior presacral vertebrae** Not sutured or fused to following centrum (0); sutured to following centrum (1); fused to following centrum (2). *Mesoleptos* 0.
187. **Pachyostosis of mid-dorsal vertebrae and ribs**. Absent (0); present (1). *Mesoleptos* 0.
196. **Body shape**. Round, dorsal ribs smoothly curved (0); laterally compressed, middle and distal regions of dorsal ribs totally straight (1). *Mesoleptos* 1.
198. **Ribs**. Proximal end without anteroventral pseudotuberculum (0); proximal end with anteroventral pseudotuberculum (1). *Mesoleptos* 0.
199. **Ribs**. Proximal end without posterodorsal pseudotuberculum (0); proximal end with posterodorsal pseudotuberculum (1). *Mesoleptos* 0.
200. **Distally forked cloacal ribs** ('lymphapophyses'). Absent (0); present (1). *Mesoleptos* 0.
201. **Tail**. Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1). *Mesoleptos* 1.
203. **Scapulocoracoid**. Present and large (0); present but reduced (1); absent (2). *Mesoleptos* 1.
204. **Emargination on anterodorsal edge of scapula**. Absent (0); present (1). *Mesoleptos* 0.
205. **Anterior (primary) coracoid emargination**. Absent (0); present (1). *Mesoleptos* 1.
206. **Posterior (secondary) coracoid emargination**. Absent (0); present (1). *Mesoleptos* 1.
207. **Clavicle**. Present (0); absent (1). *Mesoleptos* 0 (see text for discussion of identity of this element).
209. **Clavicles**. Rod-like, at most only slightly expanded proximally and with no notch or fenestra (0); greatly expanded proximally, usually with notch or fenestra (1). *Mesoleptos* 0 (see text for discussion of identity of this element).
218. **Forelimbs**. Large (0); small (1), absent (2). *Mesoleptos* 1.
222. **Pelvis**. Present and large (0); present and small (1); absent (2). *Mesoleptos* 1.
228. **Hindlimbs**. Well-developed (0); reduced (1); absent (2).

Mesoleptos 1.

234. **Body proportions**. Head moderately large with respect to wide trunk region (0); head extremely small with respect to wide trunk region (1). *Mesoleptos* 1.
235. **Dorsal body osteoderms**. Absent (0); present (1). *Mesoleptos* 0.
236. **Ventral body osteoderms**. Absent (0); present (1). *Mesoleptos* 0.
246. **Epiphyses**. Present on appendicular and axial skeleton (0); present on appendicular, but absent on axial skeleton (1); absent from both appendicular and axial skeleton. *Mesoleptos* 1. Note *Haasiophis* was incorrectly coded with state 1 in Lee (2002); it has state 2.

Appendix 2 Synapomorphies for Clades A–D in Fig. 3A

Character number, consistency index and direction of change (if not 0 → 1) listed in parentheses.

Clade A: dolichosaurs, *Adriosaurus*, *Mesoleptos*, and *Ophidia*

*More than ten cervical vertebrae (181, 0.6, 2→3), *Scapulocoracoid reduced (203, 0.67), *interclavicle absent (210, 0.33), *forelimbs small (218, 0.5), *pelvis reduced (222, 0.5), *hindlimbs small (228, 0.67).

Clade B: *Adriosaurus*, *Mesoleptos*, and *Ophidia*

*Premaxilla-maxilla contact mobile (5, 1.0), frontals paired (26, 0.14), postorbitofrontal ventral process large (36, 0.5, 1→0), supratemporal superficial (52, 0.67, 1→0), *body laterally compressed (196, 0.5), pubis not expanded distally (227, 1.0).

Clade C: *Mesoleptos* and *Ophidia* (snakes)

*Vertebral condyles facing posteriorly (172, 1.0, 1→0), *head small with respect to trunk (234, 1.0).

Clade D: *Ophidia* (snakes)

Dorsal process of maxilla on middle or anterior of maxilla (8, 0.5, 1→0), posterior process of maxilla long (10, 0.33, 1→0), lacrimal absent (11, 0.5), frontoparietal suture with sinuous contact (30, 0.2, 1→0), pineal foramen absent (40, 0.17), parietal table reduced to sagittal crest (42, 0.22, 1→0), suspensorial ramus of parietal reduced (44, 0.5), upper temporal arch incomplete (45, 0.25), tympanic crest absent (57, 0.29, 0→2), parietal downgrowths contacting parabasisphenoid (67, 1.0), optic foramina enclosed in bone (68, 1.0), anterior brain cavity floored by frontals and cultriform process (69, 0.67, 0→2), trigeminal foramina bordered at least partly by parietal (70, 1.0), supraoccipital on skull roof behind parietal (86, 0.5), posttemporal fenestra closed (89, 0.5), opening of Jacobson's organ enclosed by vomer and septomaxilla only (94, 0.4, 1→2), vomer medial to palatine (99, 1.0), palatine-vomer contact mobile (102, 1.0), palatine long (103, 0.33, 1→0), palatine with distinct rectangular process (105, 1.0), two or fewer mental foramina on lateral surface of dentary (117, 1.0), posterior margin of lateral surface of dentary deeply notched (123, 0.4, 1→2), dentary overlapped by surangular (124, 1.0, 0→2), surangular extends far over lateral surface of dentary (134, 1.0, 2→3), articular fused with prearticular and surangular (144, 0.25, 1→0), retroarticular process short (145, 1, 0→1), marginal teeth with medial and lateral carinae (153, 0.67, 1→2), palatine teeth present (166, 0.33, 1→0), palatine teeth long fangs (167, 1.0), *at least 120 presacral vertebrae (180, 0.6, 3→5), *lymphapophyses present (200, 0.67), *shoulder girdle absent (203, 0.67, 1→2), *clavicle absent (207, 0.33), ossified sternum absent (213, 1.0), *forelimbs absent (218, 0.5, 1→2), scleral ossicles absent (241, 0.5), *appendicular epiphyses absent (246, 0.67, 1→2).